

Zonation and Behavioral Patterns of the Intertidal Gastropods *Nodilittorina* (*Tectininus*) *antoni* (Philippi, 1846) and *Nerita versicolor* Gmelin, 1791, in the Bahamas

by

PAULETTE PECKOL AND SHEILA GUARNAGIA¹

Department of Biological Sciences, Smith College, Northampton, Massachusetts 01063, U.S.A.

AND

MARCIA FISHER

Department of Biology, Amherst College, Amherst, Massachusetts 01002, U.S.A.

Abstract. The herbivorous tropical gastropods *Nerita versicolor* Gmelin, 1791, and *Nodilittorina* (*Tectininus*) *antoni* (Philippi, 1846) have an overlapping vertical distribution on intertidal, rocky shores of the Bahamas. Zonation and behavioral patterns of these mollusks were examined in relation to the tidal gradient, microhabitat characteristics, and the occurrence of the other snail species. Densities of the two gastropods at low tide were negatively correlated ($P < 0.05$) at sites etched with numerous, small pits. At these sites, the smaller snail, *Nodilittorina antoni*, predominated in the high zone; the larger *Nerita versicolor* was rare in high zones at all sites except one that lacked such small pits. *Nodilittorina antoni* rarely occurred below the high-mid zone at any sites. Observed distribution patterns were re-established following transplant of marked snails outside their respective zones, both in the presence and absence of the other species. Both gastropods, particularly *Nodilittorina antoni*, were most abundant in crevices or pits during daytime low tides, a period of inactivity. Continual emergence and submergence experiments indicated that vertical ranges of both species were well within physiological tolerances. Gut analyses indicated that the gastropods had a similar diet of cyanobacteria, which predominated throughout their vertical range. The shore-level gradients of snail size and density, as well as behavioral patterns, suggest an active response to microhabitat characteristics and, possibly, predation pressure.

INTRODUCTION

Experimental work on rocky shores has revealed the importance of both physical and biotic processes in regulating density and distribution of intertidal gastropod populations. Desiccation and heat stress, particularly critical during low tides in tropical environments (MOORE, 1972), affect snail behavior, resulting in limited cyclic activity (SAFRIEL, 1969; HUGHES, 1971; Warburton, 1973; RUWA

& BRAKEL, 1981; GARRITY, 1984), selective use of microhabitats (GARRITY, 1984), evaporative cooling (VERMEIJ, 1971, 1973), formation of multilayered aggregations (GARRITY & LEVINGS, 1984), and establishment of shore-level size gradients (FRANK, 1965; VERMEIJ, 1972). Gastropods may also aggregate in response to distribution of food resources (UNDERWOOD, 1976), and shore-level size gradients sometimes reflect selective predation (VERMEIJ, 1972; MCCORMACK, 1982). In tropical environments, competition (UNDERWOOD, 1976, 1978; BLACK, 1979; ORTEGA, 1985) and predation (BERTNESS *et al.*, 1981; BERTNESS & CUNNINGHAM, 1981; GARRITY & LEVINGS,

¹ Present address: 30 Alaric Street, West Roxbury, Massachusetts 02132, U.S.A.

1981, 1983; MENGE & LUBCHENCO, 1981; CHILTON & BULL, 1984) may strongly affect abundance patterns of gastropods. While these and other results (RUWA & JACCARINI, 1986) emphasize the varied responses possible for mobile intertidal organisms, surprisingly few studies have focused on physiological or behavioral responses of gastropods following transplant above or below their natural vertical range. The present study examines an aspect of the proximate mechanism that results in the maintenance of shore-level gradients in gastropods.

The herbivorous gastropod genus *Nerita* is common throughout the tropics and subtropics, and zonation of most species reflects the tidal gradient (VANNINI & CHELAZZI, 1978; GARRITY & LEVINGS, 1981; RUWA & JACCARINI, 1986). *Nerita versicolor* Gmelin, 1791, whose geographic range includes Bermuda and south Florida to Brazil (EMERSON & JACOBSON, 1976; ABBOTT, 1986), is usually characteristic of high-shore locations during low tide (HUGHES, 1971; VERMEIJ, 1973). In Caribbean waters, the littorinid gastropod *Nodilittorina* (*Tectininus*) *antoni* (Philippi, 1846) (BANDEL & KADOLSKY, 1982) joins *Nerita versicolor* on rocky shores. Although their distribution at low tide is overlapping for a portion of their vertical range, *Nerita versicolor* extends into the lower mid-intertidal zone, while *Nodilittorina antoni* usually predominates in the high intertidal zone in the Bahamas. Here, we examine snail abundance and distribution in response to the tidal gradient and microhabitat characteristics. We seek to determine whether zonation and behavioral patterns of these prosobranch gastropods are related to physiological limitation, habitat characteristics, or biological interactions.

MATERIALS AND METHODS

Study Sites

In order to document snail distribution in relation to substratum heterogeneity and slope of the shore, *Nerita versicolor* and *Nodilittorina antoni* were examined at five sites in the Bahamas, all with predominantly west-facing exposure. The substratum at all sites was lithified carbonate beach sand (eolianite beachrock). The primary study area (site 1) at San Salvador Island (24°03.0'N, 74°33.0'W) had a slope of 60° and tidepools occurred throughout the intertidal zone. The rock surface was heavily pitted by small, deep depressions in high intertidal areas (60% of the surface) and became smoother in the seaward direction. Only 20% of the rock surface was pitted in low intertidal regions. An area with similar slope and microhabitat structure was studied at Man O War Cay (26°36.3'N, 77°01.0'W, site 2). Three additional sites were studied at San Salvador Island. Site 3 had a slope of 45°, decreased pitting downshore (70% and 10% of the surface in high and low intertidal areas respectively), and no tidepools. Site 4 (slope 20°) had shallow pits (60% of surface) in the mid-intertidal, while high and low intertidal areas had a relatively flat, open-faced topography. Tidepools were rare

(<5% of surface) at this site. Site 5 (slope 20°) contained deep pits (50% of surface) in high intertidal areas; low intertidal topography was predominantly tidepools alternating with ridges. Measurements were taken during January 1986 and 1987 at San Salvador Island sites and during March 1986 at Man O War Cay.

The most abundant intertidal gastropod species at all sites were the herbivorous prosobranchs *Nerita versicolor* and *Nodilittorina antoni*. Other components of the gastropod assemblage, including *Nerita peloronta* Linnaeus, *Nerita tessellata* Gmelin, and *Nodilittorina tuberculata* Menke, occurred in low abundance. The rocky substratum showed a patchy distribution (up to 30% cover) of encrusting cyanobacteria; other attached organisms (*e.g.*, barnacles and macroalgae) were rare.

Methods

Based on preliminary observations during low tide of the distribution patterns of *Nerita versicolor* and *Nodilittorina antoni* at site 1, three intertidal zones were defined for study: (1) a high zone, at approximately +1.4 m above mean low water (MLW), where *Nodilittorina antoni* predominated, (2) the high-mid zone, at approximately +0.9 m above MLW, where the two snails showed greatest overlap, and (3) the low-mid zone, at +0.5 m above MLW, where *Nerita versicolor* predominated. Height measurements were made with level and stadia. The zones of sites 4 and 5 were compressed vertically owing to the more gentle slope of the shore. Abundance of *Nerita versicolor* and *Nodilittorina antoni* were measured during low tide by sampling 0.09-m² quadrats ($n = 8$ to 16) located at 0.5-m intervals along a horizontal transect situated at the approximate center of each of the three zones at the five sites. Within the zones, microhabitat use was quantified by recording the characteristics of the rock on which the snails occurred, *e.g.*, pitted, tidepool, or flat.

Size-frequency distributions by zone were determined at site 1, San Salvador Island, by collecting all individuals within several 0.09-m² quadrats used for density estimates. We measured shell length (aperture to apex) to the nearest 0.1 mm using Vernier calipers.

We examined epilithic crusts in each zone at sites 1 and 4 in order to qualitatively relate microalgal abundance to snail distribution patterns. The crusts were scraped from 0.16-cm² quadrats with a razor blade and examined with a compound microscope. In addition, gut contents of both snail species were assessed. Specimens preserved in 10% formalin solution were returned to the laboratory and dissected; gut contents were examined with a compound microscope.

We determined whether the observed vertical distribution patterns were related to physiological limitation, *i.e.*, desiccation or intolerance of long-term submergence. Plastic containers (20 × 20 × 6 cm), from which the bottoms were removed, were fastened to the rocky substratum with masonry nails at 0.0 m (below the range of

Table 1

Relative proportions of *Nodilittorina antoni* and *Nerita versicolor* in different microhabitats during daytime low tide at San Salvador Island, Bahamas. Data were pooled for sites 1, 3, 4, and 5 across tidal zones.

Species	n	Microhabitat type		
		Flat	crevice/pit	Tidepool
<i>Nodilittorina</i>	1656	0.17	0.81	0.01
<i>Nerita</i>	563	0.34	0.60	0.06

either species) and at +1.7 and +2.0 m (above the range of either species). Individuals of both species were enclosed in the containers, which were covered by screen (mesh size = 4 mm). The shading from the screen reduced the midday substratum temperature approximately 1.5°C relative to the adjacent rock surface. Snail survivorship ($n = 20$, each treatment) was determined after six days. In addition, snails were held submerged in running seawater (in the laboratory) or emerged in open containers receiving midday sun in order to determine tolerance of continual submergence ($n = 50$, each species) and emergence ($n = 50$, each species) respectively. Loss of fresh weight by marked individuals ($n = 10$, each species) held in the open containers was determined daily for six days.

Transplant experiments were designed to assess snail movement in relation to tidal height and the presence or absence of the other snail species. Snails were collected throughout their vertical range at sites 1 and 2. The shells were numbered in the laboratory with indelible ink (*Nerita*) or with a numbered 2 × 2-mm tag glued to the shell (*Nodilittorina*); clear Superglue® sealed the markings. Although marked *Nerita* had the same size distribution as the natural population, the mean size of marked *Nodilittorina antoni* was greater than the natural population owing to difficulties of marking very small snails. The snails were returned to the site at the next low tide, placed on wetted rock surfaces in the high and low-mid zones at naturally occurring densities. For *Nodilittorina antoni*, snails returned in the high zone were within their vertical range (control treatment), but above the range of *Nerita versicolor*, while snails placed in the low-mid zone were below their vertical range, but within the range of *Nerita versicolor*. The opposite transplant conditions were true for *Nerita versicolor*. The effect of interspecific interactions on movement patterns was determined by comparing response of snails placed into areas where the other species occurred in natural abundances with a removal treatment. For this latter treatment, *Nerita versicolor* and *Nodilittorina antoni* were removed from experimental areas (ca. 6 m²) within the low-mid and high zones, respectively, where the other species had been placed. This method of snail removal was effective for the duration of the experiment; the few (<5 per m²) immigrating snails were removed daily from each

area. Location of marked snails was determined after two and six tidal cycles (site 1) or one tidal cycle (site 2).

One-way analysis of variance (ANOVA) or *t*-tests were used to establish significant differences for means of density and weight loss measurements; Mann-Whitney *U*-tests were used for comparisons of size-frequency distributions (Sokal & Rohlf, 1981). The Student-Newman-Keuls (SNK) procedure was applied to significant ANOVA tests. The relationships between time and weight loss and between microhabitat features and snail density were determined using linear regression. Chi-square analyses established the significance of movement patterns following various transplant conditions.

RESULTS

Zonation Patterns

Microhabitat selection: Observations made during falling and incoming tides revealed that both species were inactive once the water dropped below their vertical position on the rock, and usually did not move again until splashed by rising water. During daytime low tides, the highest proportion of both species, particularly *Nodilittorina antoni* (hereafter as *Nodilittorina*), were lodged in crevices or pits (Table 1). Results from regression analysis revealed a significant positive relationship ($r^2 = 0.79$, $F = 14.9$, $P < 0.02$) between snail density and occurrence of pits in the high zone for *Nodilittorina*. While density of *Nerita versicolor* (hereafter as *Nerita*) was negatively related ($r^2 = 0.90$, $F = 34.1$, $P < 0.01$) to the occurrence of pits in the high zone, snail number and substratum pitting were positively correlated ($r^2 = 0.79$, $F = 11.0$, $P < 0.05$) in the high-mid zone. One-third of the sampled *Nerita* were also found on relatively flat rock; this surface occurred predominantly in the low-mid zone. Few snails occurred in tidepools despite the relatively high abundance of this microhabitat throughout the range of both of these snails.

Slope of the shore had limited effect on snail distribution patterns at low tide. *Nodilittorina* density was not related to slope of the shore except in the high zone ($r^2 = 0.96$, $F = 87.6$, $P < 0.001$). There was no apparent relationship ($P > 0.05$) between *Nerita* density and shore inclination in any of the zones.

Size gradients and abundances: Mean size of *Nodilittorina* and *Nerita* increased significantly in the downshore direction at site 1 (Figure 1). For example, during January 1986 and 1987, mean size of *Nerita* was greater ($P < 0.01$, Mann-Whitney *U*-test) in the low-mid than high-mid zones. Mean size of *Nodilittorina* was greater ($P < 0.05$, Mann-Whitney *U*-test) during 1987 than 1986 at both tidal levels, concomitant with a significant decrease in size of *Nerita* during the same period in the high-mid zone, the area of overlap.

Distinctive abundance patterns with tidal height were evident for both species at sites 1, 2 and 3 (Table 2). *Nodilittorina* rarely occurred in the low-mid zone while

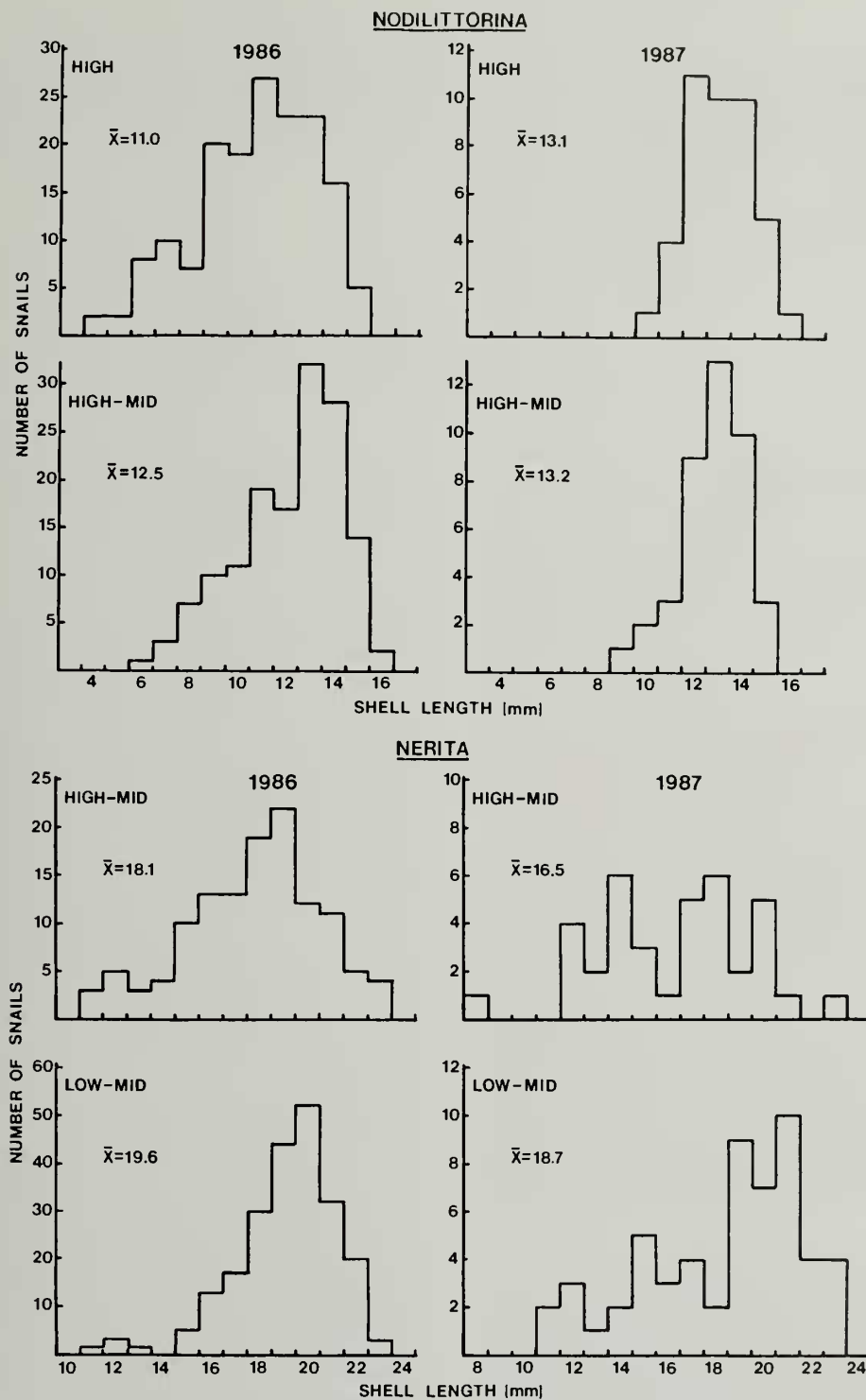


Figure 1

Size-frequency distributions of *Nodilittorina antoni* and *Nerita versicolor* with tidal height during January 1986 and 1987 at site 1. Mean (\bar{x}) size (mm) is indicated for each zone.

Table 2

Densities (mean number \pm SE per m²) of *Nodilittorina antoni* and *Nerita versicolor* by zone at five sites in the Bahamas. Sampling dates: site 1, January 1986 and 1987; site 2, March 1986; sites 3–5, January 1987.

Zone	Species	Site 1		Site 2	Site 3	Site 4	Site 5
		1986	1987				
High	<i>Nodilittorina</i>	259 \pm 71	240 \pm 49	312 \pm 109	201 \pm 50	18 \pm 4	32 \pm 6
	<i>Nerita</i>	0	4 \pm 2	0	0	44 \pm 10	11 \pm 4
High-mid	<i>Nodilittorina</i>	110 \pm 58	95 \pm 28	46 \pm 19	116 \pm 38	272 \pm 56	78 \pm 18
	<i>Nerita</i>	36 \pm 11	29 \pm 7	30 \pm 9	11 \pm 6	56 \pm 11	57 \pm 9
Low-mid	<i>Nodilittorina</i>	0	6 \pm 4	0	0	16 \pm 6	3 \pm 1
	<i>Nerita</i>	56 \pm 16	31 \pm 12	124 \pm 41	33 \pm 14	6 \pm 4	72 \pm 16

Nerita was usually absent from the high zone at these sites. Except for the 1987 sample of *Nerita* at site 1, both species had lower densities ($P < 0.05$, t -tests) in the high-mid zone, the area where they showed greatest overlap. In fact, densities of the two species were negatively correlated at the three sites (Pearson product-moment correlation coefficients: site 1, $r = -0.28$, $P < 0.05$; site 2, $r = -0.51$, $P < 0.01$; site 3, $r = -0.47$, $P < 0.01$). Although densities of *Nodilittorina* at site 1 were similar during 1986 and 1987, *Nerita* was less abundant during 1987 than 1986.

Snail distribution patterns at sites 4 and 5 contrasted with those of the other sites (Table 2). *Nodilittorina* was more abundant ($P < 0.05$, SNK) within the high-mid zone, particularly of site 4, rather than the high zone. In fact, there were significantly fewer *Nodilittorina* in the high zone at sites 4 and 5 than at the other three sites. *Nerita* had relatively high abundance in the high zone, and low density in the low-mid zone at site 4 ($P < 0.05$, SNK), a reversal of its distribution pattern at all other sites.

Food availability: Crusts scraped off the rocks from the three zones at sites 1 and 4 indicated that cyanobacteria, particularly *Oscillatoria* sp., *Calothrix* sp., and *Anacystis* sp., predominated throughout the vertical range of the two gastropods. Qualitative (visual) estimates indicated that biomass of these encrusting species was inversely related to tidal height. Gut contents of *Nodilittorina* and *Nerita* were similar, and reflected the relative abundances of the cyanobacteria.

Response to Transplant Conditions

Continual submersion and emersion: Results of the continual submergence and emergence tests indicated that *Nodilittorina* and *Nerita* had a vertical distribution at low tide that was well within their physiological range. For example, both species survived one week of continual submergence. All snails survived within enclosures placed above their vertical ranges; however, *Nodilittorina* had greater percentage weight loss ($P < 0.001$, t -test) than *Nerita* after a 24-h period of continual emergence. Following this initial water loss, both species had the same rate of weight loss

for the next five days (slopes of both linear regressions, $b = 0.03$, for days two through six; Figure 2). Enclosures placed below the range of either species were removed by heavy wave action during a storm.

Movement patterns: Results from the control treatments for the transplant experiments of *Nerita* and *Nodilittorina* indicated little effect from handling the snails (Table 3). At site 2, 100% of both species that were marked and replaced in their respective zones were recovered. The mean recoveries of snails from the control treatment during the two transplant experiments at site 1 were 89% and 88% for *Nerita* and *Nodilittorina* respectively.

Snail movement patterns following transplant were independent of occurrence ($P > 0.10$, Chi-square tests) of the other species (Table 3). For example, at site 2, all recovered *Nerita* and *Nodilittorina* that had been transplanted to the high-mid and low-mid zones respectively, showed similar movement patterns in the presence and absence of the other species. Thus, for subsequent statistical analyses and discussion, we pooled those data, and focused on assessing snail response to placement at various tidal locations.

Recovery location following transplant was, in part, dependent on the length of time between initiation of the experiment and subsequent sampling (Table 3). Snails placed in the zone where they had highest natural abundance were usually recovered in the same zone, regardless of the time interval following placement. The exceptions, three *Nerita* that moved into a high intertidal pool following placement in the low-mid zone, remained there for the duration of this experiment. At site 1, 28% (during 1986) and 40% (during 1987) of *Nerita* transplanted into the high zone (above its usual range) remained there after two tidal cycles. However, for the 1987 transplant experiment, 26% of those snails recovered in the high zone were located in tidepools. Similarly, 21% (during 1986) and 23% (during 1987) of *Nodilittorina* transplanted into the low-mid zone (below its usual range) remained there after two tidal cycles. At site 2, all recovered *Nerita* transplants had returned downshore to their natural zone after one tidal

cycle, while less than one-half of the transplanted *Nodilittorina* had moved upshore to their zone within the same period. After six tidal cycles at site 1, all but one recovered *Nodilittorina* transplant had returned upshore; the only *Nerita* remaining in the high zone after this period were located in tidepools.

DISCUSSION

This study documented site-specific zonation patterns of *Nerita versicolor* and *Nodilittorina antoni* in the Bahamas. Although *Nerita* is characteristic of high-shore locations on both horizontal and vertical surfaces (HUGHES, 1971; VERMEIJ, 1973), in the present study this species extended above the high-mid zone only at a site with reduced microtopography, where *Nodilittorina* was less abundant. *Nerita* was extremely rare in high zones of sites etched with small pits. In contrast, *Nodilittorina* predominated in high-shore regions but was rarely observed below the high-mid zone. In fact, interspecific densities were negatively correlated at three sites. This zonation pattern was re-established following transplant of the snails outside of their vertical range. The zonation and behavioral patterns of these intertidal gastropods thus suggest an active response to microhabitat characteristics or species interactions.

Based on continual emersion and submersion tests, the vertical distribution of both snails at low tide was well within their physiological limits. The nodulose shell sculpture of many high intertidal littorinids, including *Nodilittorina*, may aid in heat loss from the shell surface (VERMEIJ, 1971, 1973). Neritid gastropods are also well-adapted to high temperature and desiccation stresses owing to their morphology and behavior. Many species have a large extravisceral reservoir, capable of holding water used in evaporative cooling. Increased shell globosity, as characteristic of *Nerita versicolor*, both enhances water-holding capacity and decreases the area and perimeter of the base in contact with the substratum. Most nerites can enter into a dormant state fully retracted into the shell behind a thick operculum (VERMEIJ, 1973). Thus, absence of *Nerita versicolor* from the high zone of most sites was probably not due to physiological limitation.

Nerita and *Nodilittorina* were inactive once water retreated during daytime low tides, and occurred predominantly in pits or crevices during this period. Use of crevices as refuges by gastropods on tropical rocky shores reduces the risk of mortality due to desiccation or heat stress (LEVINGS & GARRITY, 1983; GARRITY, 1984). RAFFAELLI & HUGHES (1978) reported a positive relationship between abundance of littorinid gastropods and the availability of crevices, and suggested that snails without this refuge were often dislodged by wave action. In the present study, either of these factors might, in part, explain the lower abundances of *Nodilittorina* in regions such as high shore at site 4 and low intertidal areas, where such microtopography was lacking. Because the two species varied greatly in size, the small, deep pits characteristic of the high intertidal

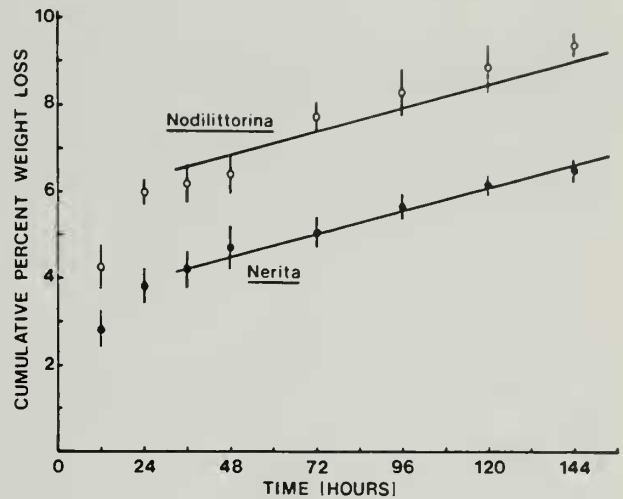


Figure 2

Cumulative percent weight loss with time (mean values \pm SE) of *Nodilittorina antoni* and *Nerita versicolor* during continual exposure to air. After 24 h, linear regression analyses generated the following equations: for *Nodilittorina* $y = 0.03x + 5.29$; for *Nerita* $y = 0.03x + 3.32$.

regions in four of the five sites may not accommodate most *Nerita*. Perhaps *Nerita* is dislodged from such highly irregular surfaces by wave action.

FLETCHER & UNDERWOOD (1987) documented a complex relationship among substratum heterogeneity, competitive interactions between two limpet species, and grazing urchins. On smooth substrata, "bulldozing" by the larger congener and crushing by grazing urchins reduced densities of the smaller limpet, *Patelloida mufria*; this interaction did not occur on pitted surfaces. In the present study, the site-specific zonation patterns of *Nerita* and *Nodilittorina*, the significant negative correlations between interspecific densities at pitted sites, the concomitant decrease in size of *Nerita* with increase in size of *Nodilittorina* during 1987 at site 1, and the regular spacing pattern ($P < 0.05$, nearest neighbor analysis, CLARK & EVANS, 1954) documented for each species in the region of overlap (Peckol, unpublished data) suggest a species interaction mediated by microhabitat characteristics.

Because snails returned to their respective zones following transplant outside their vertical range both in the presence and absence of the other species, it is unlikely that distribution patterns are due to interference competition. Intra- and interspecific competition for food have been shown to affect density and growth of intertidal gastropods (HAVEN, 1973; UNDERWOOD, 1976; LEVINTON, 1985). Gut analyses indicated that the two snails in this study have a similar diet, primarily cyanobacteria. Although UNDERWOOD (1978) suggested that the radular design of neritid gastropods permitted rapid, effective foraging of the surface microalgae, possibly *Nerita versicolor* does not forage

Table 3

Recovery of *Nodilittorina antoni* and *Nerita versicolor* after one to six complete tidal cycles following transplant of snails within and outside their vertical range in the presence (+) and absence (-) of the other species at sites 1 (San Salvador Island) and 2 (Man O War Cay). For *Nodilittorina*, within = high and high-mid zones, outside = low-mid zone; for *Nerita*, within = high-mid and low-mid zones, outside = high zone. TP = snail found in a tidepool within a particular zone.

Transplant condition		n	Percent recovered	Number recovered	
				Within zone	Outside zone
Site 1:					
January 1986, 2 tidal cycles					
<i>Nodilittorina</i>	Within zone	37	84	31	0
	Outside zone (+)	38	84	24	8
<i>Nerita</i>	Within zone	40	80	32	0
	Outside zone (+)	40	84	22	11
January 1987, 2 tidal cycles					
<i>Nodilittorina</i>	Within zone	33	92	30	0
	Outside zone (+)	30	97	21	8
	Outside zone (-)	32	100	26	6
<i>Nerita</i>	Within zone	31	94	26	3 (TP)
	Outside zone (+)	36	92	16	11 + 6 (TP)
	Outside zone (-)	32	94	18 + 2(TP)	9 + 1(TP)
January 1987, 6 tidal cycles					
<i>Nodilittorina</i>	Within zone	33	78	26	0
	Outside zone (+)	30	80	24	0
	Outside zone (-)	32	100	31	1
<i>Nerita</i>	Within zone	31	84	23	3 (TP)
	Outside zone (+)	36	78	26	2 (TP)
	Outside zone (-)	32	72	23	0
Site 2:					
March 1986, 1 tidal cycle					
<i>Nodilittorina</i>	Within zone	50	100	50	0
	Outside zone (+)	50	88	19	25
	Outside zone (-)	50	90	21	24
<i>Nerita</i>	Within zone	29	100	29	0
	Outside zone (+)	50	94	47	0
	Outside zone (-)	50	82	41	0

effectively over deeply pitted surfaces characteristic of the high zones of several sites. Larger snails often move greater distances than smaller individuals during foraging activities (RUWA & BRAKEL, 1981; LEVINGS & GARRITY, 1983; GARRITY & LEVINGS, 1984). Thus larger *Nerita versicolor* may forage greater distances, enabling the species to benefit from the more abundant food resource of the lower intertidal region.

In addition to density differences along the tidal gradient, both species showed an inverse relationship between tidal height and shell size. Selective predation in lower intertidal areas might result in this size gradient (VERMEIJ, 1972; CHILTON & BULL, 1984). The impact of predatory fish, crabs, and snails on foraging patterns and survival of tropical gastropods has been investigated (SAFRIEL, 1969; HUGHES, 1971; BERTNESS *et al.*, 1981; GARRITY & LEVINGS, 1981, 1983). Although size selection by predatory crabs has been documented (ELNER & HUGHES, 1978; BERTNESS & CUNNINGHAM, 1981; CHILTON & BULL,

1986), BERTNESS *et al.* (1981) found that fish crushed the largest (20.5 mm) neritid gastropod offered. Additional work is necessary in order to determine if selective predation contributes to the intra- and interspecific shore-level size gradients observed in this study.

The shore-level gradients of size and density maintained by intertidal gastropod populations in response to food or microhabitat availability, or to selective predation, are clearly finely tuned relative to zonation patterns of sessile organisms. The variations in distribution patterns with site, documented in this study, and time (RUWA & BRAKEL, 1981; LEVINGS & GARRITY, 1983; RUWA & JACCARINI, 1986) emphasize the dynamic nature of processes operating in rocky intertidal, particularly tropical, habitats.

ACKNOWLEDGMENTS

We thank College Center of the Finger Lakes Bahamian Field Station at San Salvador Island, Bahamas, for labo-

ratory support. Funding was provided by Smith College (to S.G. and P.P.) and by the Five College Coastal and Marine Sciences Program (to P.P.). This paper was improved through critical reading by S.C. Levings and two anonymous reviewers.

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